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Grazers, pathogens and shelf-shading enhance phytoplankton species richness more and reduce productivity less when environments are less dynamic: A theoretical study

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ABSTRACT

Human activities, such as reservoir construction, can result in hydraulically less dynamic systems and cause downstream systems to shift from sudden resource supply transitions to gradual. In this research, how such human activities might influence phytoplankton is further explored theoretically. Building on previous modeling results, new findings suggest that preferential grazing, pathogens, self-shading, and all these combined interact differentially with the mode of resource loading (sudden and gradual transitions) to shape phytoplankton assemblage characteristics. Most notably, phytoplankton species richness was much greater in scenarios that considered pathogen effects, self-shading effects, and combined preferential grazing, pathogen and shelf-shading effects when resource supply transitions were gradual compared to when they were sudden, i.e., 2.7-fold increase, 2.4-fold increase and 1.7-fold increase, respectively. Furthermore, reduced productivity with the additions of preferential grazing, pathogens, self-shading, and all these combined was lessened when resource supply transitions were gradual. Smaller differences to phytoplankton species evenness, overyielding, species interactions, niche breadth, and resource drawdown were also observed when comparing scenarios with sudden and gradual resource supply transitions. The nuanced details of preferential grazing, pathogens and shelf-shading uncovered here underscore the fundamental principle framed in the philosophy of Okham's Razor. How much complexity must we account for to understand how plankton systems will respond to altered land use in watersheds, and associated changed hydrology and nutrient loading? In this cursory effort, with simplistic additions of preferential grazing, pathogens and self-shading, findings highlight the need to explore empirically the effects of impoundment construction on downstream estuarine ecosystems.

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1. Introduction

Coastal marine systems sometimes experience alternating periods of reproductive growth limitation within an annual cycle (Caraca, 1988; Webb, 1987; Fisher et al., 1992; Yin, 2002; Yin et al., 2004; Pilkaityte and Razinkovas, 2007). Transitions between these periods can be sudden, as expected in systems influenced by pulsed inflows (Tamvakis et al., 2012; Roelke et al., 2013; Roy et al., 2013; Morse et al., 2014) or wind-driven mixing events (Lares et al., 2009; Hu et al., 2011; Chen et al., 2013). Transitions can also be gradual, as

expected in systems influenced by seasonally developing wet and dry periods, or annually occurring periods of upwelling (Anabalón et al., 2014; Zhou et al., 2014). Human activities in the Anthropocene, such as reservoir construction, can result in hydraulically less dynamic systems, i.e., smaller magnitude spates and protracted periods marginally above historical baseline flows (Magilligan and Nislow, 2005; Poff et al., 2007). In turn, these altered flows might cause systems to shift from sudden resource supply transitions to gradual, a notion as yet undocumented primarily due to lack of reliable, watershed-scale, pre-impoundment nutrient loading data. Nonetheless, the question of how such human activities and resulting alterations to inflow and nutrient loading might influence phytoplankton succession and assemblage characteristics is worth exploring as continued impoundment construction is ongoing in

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many watersheds globally (Winemiller et al., 2016).

Recently, multi-nutrient, multispecies models were employed to compare how sudden and gradual transitions in resource supplies (nutrient loading) influences the succession patterns and characteristics of self-organized phytoplankton assemblages (Roelke and Spatharis, 2015a,b). Those studies found that the differences between systems characterized by sudden and gradual resource supply transitions were dependent on the level of complementarity within phytoplankton assemblages, where complementarity referred to increased use of growth-limiting resources when certain species, or clusters of species, co-occurred. In the extremes, phytoplankton species richness and transgressive overyielding increased when complementarity was lowest, and phytoplankton biomass increased when complementarity was highest. For low-complementarity simulations, the persistence of intermediate-performing species led to higher richness and overyielding. For high-complementarity simulations, the formation of species clusters and niche compression enabled higher biomass accumulation.

The findings of Roelke and Spatharis (2015a,b) suggest that an understanding of factors influencing the emergence of life history traits important to complementarity is necessary to predict the impact of watershed development on phytoplankton productivity and assemblage structure, assuming that altered flows resulting from impoundment construction cause systems to shift from sudden resource supply transitions to gradual. Those studies, however, did not account for other processes that shape phytoplankton assemblage structure, such as preferential grazing, pathogens and self-shading. For example, preferential grazing was shown to influence both phytoplankton community composition and productivity, where differences in phytoplankton cell size and morphology led to differential edibility (Gaul and Antia, 2001; Katechakis et al., 2002; Winder et al., 2012). Regarding pathogens, virus and algicidal bacteria are also known to influence phytoplankton composition and productivity, in some cases leading to abrupt termination of blooms (Bratbak et al., 1993; Fuhrman, 1999; Mayali et al., 2008). Finally, self-shading, a phenomenon where accumulated phytoplankton biomass brings about light limitation, was shown to influence spring bloom cycles and limit productivity (Townsend et al., 1994; Mellard et al., 2012). Because the structure of the model used in Roelke and Spatharis (2015a,b) did not account for preferential grazing, pathogens or self-shading, findings from those studies might have fallen on the overly-shaved side of Ockham's Razor, i.e., too simple.

In this research, a cursory assessment of preferential grazing, pathogens and self-shading effects on phytoplankton assemblages is conducted through expansion of the model presented in Roelke and Spatharis (2015a,b). The model still depicts plankton systems that experience recurrently fluctuating resource supplies, where the phytoplankton self-organize into stable assemblages, but is now expanded to include preferential grazing, pathogens or self-shading effects, as well as all three processes combined, producing four new models of greater complexity. The goal of the research reported here is not to provide an exhaustive exploration of the models' potential parameter spaces. For example, temporally varying hydraulic residence times (Örnólfsson et al., 2004; Roelke et al., 2013, 2017; Dorado et al., 2015; Hitchcock et al., 2016; Zhang et al., 2016), migration effects in spatially heterogeneous systems (Messie and Chavez, 2017; Sauterey et al., 2017; Sommer et al., 2017), and temperature and salinity sensitive plankton life history traits (Ketchum, 1951, 1954; Mutshinda et al., 2017; Skau et al., 2017), which are all important mechanisms influencing marine plankton systems, are not considered here. But rather, the goal of the research is to theoretically illustrate how preferential grazing, pathogens, self-shading and all these processes combined might

interact with the mode of resource loading transitions (sudden and gradual) to shape phytoplankton assemblages, which in turn may better inform future empirical studies that test how well these theoretical insights hold up in reality.

2. Methods

2.1. Modeling approach

Briefly, the Roelke and Spatharis (2015a,b) model, which will now be referred to as the base model for this research, is a multi-nutrient, multispecies mathematical model used to explore how nutrient loading switching mode, i.e., sudden vs. gradual transitions in the concentration of nutrients in the supply, effects phytoplankton succession and assemblage characteristics. The base model is governed by the widely-used Monod-relationship (Monod, 1950), which predicts an instantaneous reproductive growth rate from ambient inorganic nutrient concentrations (Fig. 1a), and is commonly used to depict population dynamics of plants, macroalgae and phytoplankton (Leon and Tumpson, 1975; Tilman, 1982; Grover, 1997). Liebig's Law of the Minimum (De Baar, 1994) is used to determine which inorganic nutrient is limiting to each species at any point during model simulations. These relationships are combined with a population loss factor, i.e., hydraulic displacement of cells associated with inflows, to determine the resource concentration above which accumulation of biomass occurs and below which it does not, denoted as the R^* (Fig. 1a), that when extended into a two-dimensional resource trade-off space defines the zero-net growth isocline (Fig. 1b). This simplistic model is the driving force for the R^* framework of understanding (Tilman, 1977, 1982), which is detailed more below, and has been a staple of plankton models for 40 years.

The model simulations employed in this research involve phytoplankton assemblages that self-organize from an initial species-rich pool of 300 (Roelke and Eldridge, 2008). In previous studies, which species survived the self-organization process was determined by their competitive abilities for two resources (Roelke and Eldridge, 2008; Roelke and Spatharis, 2015a,b). In addition, the Roelke and Spatharis (2015a,b) papers explored many levels of complementarity spanning from low to high. In this research, which species survive the self-organization process is determined by their competitive abilities for two resources as well as their resistance to grazing; vulnerability to pathogens; degree to which they become light-limited through self-shading; and grazing, pathogens and self-shading effects combined. Also, in this research an intermediate level of complementarity (distribution of species' R^* s, *sensu* Tilman, 1982, through the resource trade-off space is moderately downward curved) is used as it is more strongly supported by experimental data on phosphorus-silicate and nitrate-silicate trade-offs (Huisman and Weissing, 2001a). The half-saturation coefficients for resource-limited reproductive growth (k_s , see below) and the fixed cellular content of resources (Q_s , see below) are the life history traits that differentiate competing species, as described in Roelke and Spatharis (2015a,b). The numerical procedures followed to establish the fluctuation modes in the resource supply, i.e., sudden and gradual transitions, are also described in Roelke and Spatharis (2015a,b).

The base model used in this research is structured to simulate phytoplankton assemblages where new resources arrive with inflows, and loss of cells and ambient nutrients occur through hydraulic displacement and dilution, which is a classic 'chemostat' configuration. This base model is enhanced into four different models (described further below) to depict effects of preferential grazing, pathogens, self-shading and all processes combined on the process of self-organization and the resulting phytoplankton

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